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REPRODUCTIVE RESPONSE OF NATIVE SCREWWORM (*COCHLIOMYIA HOMINIVORAX* (COQ.)) POPULATIONS TO STERILE FLY RELEASE

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Abstract.—Data were analyzed from 14 field experiments designed to test interactions between released, sterile screwworm adults and the native population. These tests provide extensive information concerning behavior and ecology of a relatively rare, inconspicuous insect. In ten tests carried out in regions not previously treated with sterile flies, egg mass deposition by native screwworms declined by an average of 43% immediately following sterile fly release. Four tests in previously treated areas did not show a decline in egg mass deposition. Aggressive mating behavior by males is hypothesized to interfere with female host-seeking activity. Predictable changes in reproductive activity may be integrated into the eradication program for scheduling use of toxic baits and rates of sterile fly release.

With the enormous diversities of habitats and species to select from, studies of insect behavior and ecology have generally centered on species that are locally abundant due to swarming behavior or localized substrates, are conspicuous due to size, coloration, or mate attracting behavior, and are of interest due to studies carried out in other disciplines or due to their economic importance. Species of economic importance also tend to be those which are least locally abundant. Those species which tend to have highly dispersed populations at low densities and are not conspicuous in most aspects of their behavior are less likely to receive attention. They are difficult to find in nature, are not likely to arouse much interest among naturalists, and usually have minimal economic impact. Among the dipterans, however, these make up a significant portion of the total species.

Diptera that can cause significant economic damage at low densities as disease vectors and parasites, such as the tsetse fly (*Glossina* spp.) and screwworm (*Cochliomyia hominivorax* (Coquillett)) may be susceptible to autocidal measures for control or eradication. Collecting sufficient ecological data to achieve this control is difficult and expensive. Extrapolation from knowledge of better studied populations is always tenuous, particularly so when the model species has been studied because it is locally abundant or conspicuous.

As the screwworm eradication program, now being executed by the Comision Mexico-Americana, has progressed to the Isthmus of Tehuantepec in southern Mexico, considerable information concerning the response of native populations, which normally have extremely low density populations, to sudden influx of sterile adults has accumulated. I present here a summary of field experiments carried out between 1953 and 1983 with respect to this response. While the primary purpose of this summary is to elucidate screwworm population ecology and behavior as a model for rare species. I hope this summary will lead to some appreciation of the extent of the efforts by various agencies to investigate screwworm biology.

Historical Considerations

The screwworm eradication program has progressed from southern United States through Mexico to the presently treated regions of eastern Mexico from the Isthmus of Tehuantepec to the Guatemala border and Yucatan peninsula. Historically, a number of proposals have been made explaining or predicting program failure, usually from a population genetics or evolution point of view. Several mechanisms have been presented as hypotheses. Smith and von Borstel (1972), citing a "genetic improvement" model of Kojima (1971), predicted that selection favoring female genotypes which discriminated against sterile males would result in native populations "that will be found near the Mexico-Texas border that will have nothing to do with the screwworms that are reared, irradiated and released."

A second type of prediction (reviewed in Bush, 1978) emphasized fitness of factory reared flies in competition with native flies for mates. These studies were mainly concerned with electrophoretic differences between factory produced and native screwworm adults. A study of α-GDH, a muscle enzyme important for flight, indicated that frequencies of two forms of this enzyme did change under mass rearing conditions. Although no in vivo tests were ever made on screwworm activity levels for the alleles, Bush et al. (1976) and Bush and Neck (1976) argued that increase in frequency in a "factory type" enzyme resulted in non-competitiveness of sterile flies.

A third hypothesis has been proposed by Richardson and Makela (1978), Richardson et al. (1982a, b) and Richardson (1982). Although details of this hypothesis have changed from one report to another, the general hypothesis is that there are distinct mating groups of screwworms which can be identified by karyotype, male genitalic morphology, and ecology. These groups, called gamodemes, are often sympatric but may be regionally distributed. For example, Richardson et al. (1982a) identified four gamodemes from Sinaloa and three others from Northern Veracruz, Mexico. From the Pacific coast of Chiapas they reported the four Sinaloa gamodemes and two of the Veracruz types. Richardson and Makela (1978) predicted that "we might expect to find a greater number of cryptic species toward the center of the screwworm's range in southern Mexico and southward." Richardson et al. (1982a) announced a total of at least nine of these groups, seven of which were reported from Chiapas. At this writing, four years after the completion of the Chiapas sampling, descriptions of these types, their frequencies and ecologies have yet to be published. The eradication program has progressed eastward through Veracruz and into Tabasco on the north coast, and through Guerrero and Oaxaca into Chiapas on the Pacific coastal regions in about 18 months. No attempts to identify mating types among the now extinct target populations have been made by either Comision Mexico-Americana or USDA support agencies.

Several of the tests described in this report were designed and executed in response to one or more of the above hypotheses. In particular, field tests of new strains for factory production have been carried out on all strains in areas scheduled for future treatment. The evidence presented by Bush and his co-workers provided a basis for the nearly regular change of factory strains from 1974 to the present on an annual basis, thus necessitating these field tests annually.

Other tests cited here were designed to test different methods of program execution, particularly patterns of sterile fly dispersal. An alternate hypothesis to explain a number of program failures, notably the 1971–73 outbreaks in Texas, was that flight lanes were too widely separated and that too many flies were being dispersed in large boxes at too distant intervals to insure adequate coverage of areas between lanes and drop sites. These hypotheses in general were proposed by personnel working within the program. While results and recommendations were published (Davis et al., 1968; Hightower et al., 1968; Krafsur and Garcia, 1978; Krafsur et al., 1980), they were only briefly mentioned, if considered at all, in the above works favoring genetic explanation for eradication problems.

Clearly, if eradication by sterile fly release is to be successful, vigorous flies must be released in proximity to the target populations and must interact with them. Experiments which address the problems of assuring that sterile flies have actually had an opportunity to mate with the target population should have priority over tests of hypotheses that the flies are not copulating due to genetic barriers. At present, proper dispersal can be checked by collecting released flies in traps located in treated regions. Matings between released males and native females are demonstrated by measuring the final result, i.e., sterility of egg masses or decline in number of screwworm cases. This type of evidence cannot separate failure in dispersal or fly vigor and failure due to genetic factors.

MATERIALS AND METHODS

Behavioral and ecological effects of massive releases of sterile factory reared flies interacting with wild populations of screwworm adults have been inferred from egg mass sterility rates, numbers of screwworm cases, and adult trapping data. Since the success of an eradication effort has been assumed to be dependent on the ratio of sterile to fertile matings, these methods of monitoring are logical and have thus far been accurate indicators of program success. The possibility that massive inundation and the following competition, courting and other interactions from sterile insects may negatively affect reproduction among native females is not necessarily reflected in percent sterility. The effects of this type of interaction, tested for *Dacus tryoni* Frogg (Tephritidae) by Monro (1966), have not been evaluated previously for insect control programs.

In order to examine the possibility of density dependent population structure in screwworm reproductive behavior, comparisons of reproductive activity before and following sterile fly release in a test area are made. In field tests of sterile fly release, total screwworm density (wild plus released) is drastically increased. Most reports of these tests evaluate effects of the sterile fly activity by measuring percent sterility of egg masses produced by wild flies. Total reproductive activity of wild flies can also be evaluated by comparing rates of egg mass deposition before and after sterile fly release or by comparing control (no release) and release areas in similar communities. Since factory reared, sterile females produce no eggs or only a few eggs, egg mass number estimates reproductive activity of wild females.

All data reviewed here are from field tests carried out by USDA agencies or the Comision Mexico-Americana para la Erradicacion del Gusana Barrenador del Ganado. In general, these studies were tests of new methods, new strains for factory production, or were for experimental examinations of screwworm biology. Areas of the tests were chosen by several criteria, high screwworm populations and accessibility for twice daily sampling being the most important. Designs and methods used in the experiments discussed here are not identical. Changes in technology between 1951 and 1983 as well as constraints imposed by habitats and research goals are reflected in the considerable variability in designs and methods used. In all tests, however, a relatively dense native screwworm population was challenged by a sudden increase in total population density due to release of sterile flies. Sterile fly release rate is standardized here as flies released per sq km. In all tests, males and females were released. In some tests corrections were made for mortality estimates before release, in others no estimates were made. Release rates are therefore only approximate. Native fly activity, estimated by egg mass deposition rate on wounded, screwworm infested sentinal animals, was monitored during the release and these data are discussed here.

Below, I summarize the various field tests used as a data base in this examination and their results. The first nine tests described below are similar in that a uninured population, that is, a population not previously treated with sterile flies, was suddenly inundated with sterile screwworm adults. The second group of tests involve populations that had been previously treated as part of the eradication program, had been treated with sterile flies previously for other tests, or had otherwise been manipulated in such a way that the adult populations were disturbed or reduced.

This sampling method may be compared to a baited trap, sampling with release, system: e.g., ovipositing females are not removed from the population, but returned to the community in slightly different condition (with fewer eggs) than when they entered the "trap." In these tests, sentinel animals occasionally died, were lost or were stolen. Local conditions also occasionally prevented certain pens from being checked as scheduled, required that pens be closed or moved, or that new pens be added. In treating these data, oviposition rate is defined as the number of masses sampled over a given period on a constant number of locations on sentinel animals. If numbers of animals changed during a test, oviposition rate was calculated as masses per pen per week. I assume that errors introduced due to daily problems in sampling or missing animals were equally distributed for treatment and control areas or for pre- and post-release sampling periods.

Populations of screwworms vary tremendously in density, even in permanently infested, coastal regions of Mexico (Spencer et al., 1983). The reproductive behavior of these insects must include not only activities for finding mates among the thousands of other sympatric blowflies, but also behavior for females to avoid courting males after they are mated in order to reduce probability of injury and loss of time when searching for oviposition sites (see Guillot et al., 1977a, b for review of this behavior). Basically I ask: does oviposition rate from a target population respond after a massive inundation of sterile flies? Second, does this change appear to be permanent or do the native flies recover from this treatment with oviposition returning to the previous level? Finally, I examine the possible mechanism of this response with respect to behavior and distribution of target (fertile) and sterile populations. This may allow application of the effects of reproductive fluctuations for implementation of the total integrated program including animal husbandry practices, adult suppression programs and the sterile fly release program.

TEST DESCRIPTIONS AND RESULTS

The first group of field experiments was executed in regions of moderate to heavy screwworm infestation in zones where sterile screwworms had not been recently, or had never been, introduced. All the tests described here were carried out with control areas outside the sterile fly treatment area or with at least some (7 days) pre-release record of egg deposition rate. There were nine tests of this sort carried out from 1953 to 1983.

Sanibel and Captiva islands.—This was the first field test of the sterile male technique for pest eradication. Oddly, the details of this test have appeared only in an "in house" USDA report (Baumhover et al., unpublished report). The test was performed during the period from January to April 1953. The area considered here consisted of Sanibel and Captiva islands, which make up part of a chain of small islands extending northward from Sanibel, Florida. The approximately 41.3 square kilometer area was treated with flies dispersed from a single engine airplane at about 77 flies/sq km weekly. Egg mass data were collected for one pre-release and 11 post-release weeks from wounded, screwworm infested goats which were used as sentinel animals. Hosts for screwworms on these islands were mainly domestic cats and dogs, feral cats, rabbits, and particularly raccoons.

While the total area treated in this experiment included a number of additional islands and mainland sites, data included here are only from three of the six sentinel animal pens which provided over 95 percent of the total 536 egg masses. These sites were the most isolated from the mainland and were always treated with the full quota of sterile flies each week.

Fig. 1 shows the number of screwworm egg masses per pen per week collected during the test. With only one week of pre-release data, interpretations are tenuous; however, the drop from 22 masses before release to 12 masses for the week following release suggests a trend in the direction of negative reproductive response of wild females to sterile fly release. There is, of course, significant probability that the decline during the second week was due solely to chance. Egg mass deposition declined as much as 50 percent twice during the sampling period, at weeks 2 and 11. Decline at week 11 probably reflected the population decline due to sterility, while decline at week 2 coincided with the introduction of sterile flies.

Curaçao Island 1954.—Eradication of screwworms from Curaçao, Netherlands Antilles, provided the first proof of the feasibility of the sterile male technique for screwworm eradication. This project involved a preliminary test from March to May 1954. Ten goat pens were stocked with four sentinel goats, two wounded and two healing, over the test period. The 440.3 sq km island was treated with sterile flies dropped in weighted paper bags, twice weekly, at a rate of 77 sterile males per sq km per week. Data were collected for 2 pre-release weeks, 1 transition week, and 6 post-release weeks. Neglected domestic goats and sheep, along with pigs, burros, deer and rabbits, were cited as most probable screwworm hosts. Complete details of this experiment and the following eradication of screwworms from Curaçao are given in Baumhover et al. (1955).

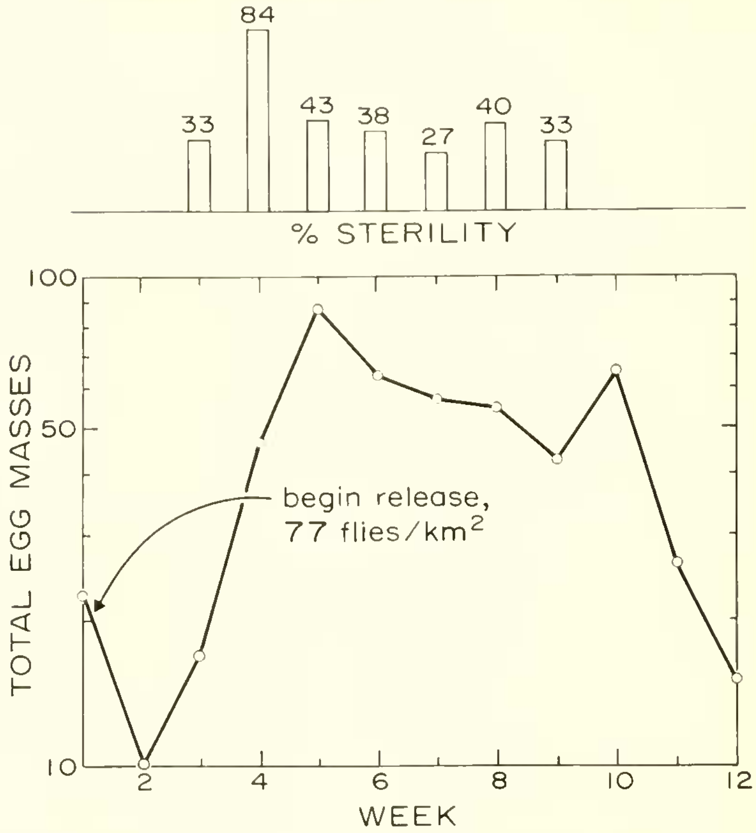

Fig. 1. Sanibel and Captiva islands, Florida. Decrease in egg mass number at 3 pens for approximately 1 week following release of sterile flies. Data are from unpublished USDA report, summarized in Baumhover et al. (1955).

Numbers of egg masses collected from sentinal goats, wounded and infested as in the Sanibel test, were recorded. Total egg masses collected per week are summarized in Fig. 2. Here, as in the Sanibel test, following sterile fly release there was a drop in oviposition rate for a brief period followed by an increase to levels above the pre-release reproductive rate. Again, sterility did not appear until the second week of release; thus the reduced oviposition was not caused by declining population size due to sterile egg masses.

This reduction, again, may be the result of chance fluctuations. The change is, however, suggestive of reproductive interference. As noted in Baumhover et al. (1955), oviposition rate on Curaçao was much greater than that during the Sanibel test. Despite this natural higher density in screwworms, an artificial increase in density of flies was associated with a temporary reduction in oviposition rate.

Central Florida 1957.—This test demonstrated the feasibility of screwworm eradication from southeastern United States, which had become infested in 1933. The experiment was carried out in 1957 to test the effects of sterile release for eradication of screwworm populations in a mainland zone where they are contiguous with a large, untreated, population. Details of this test were reported by

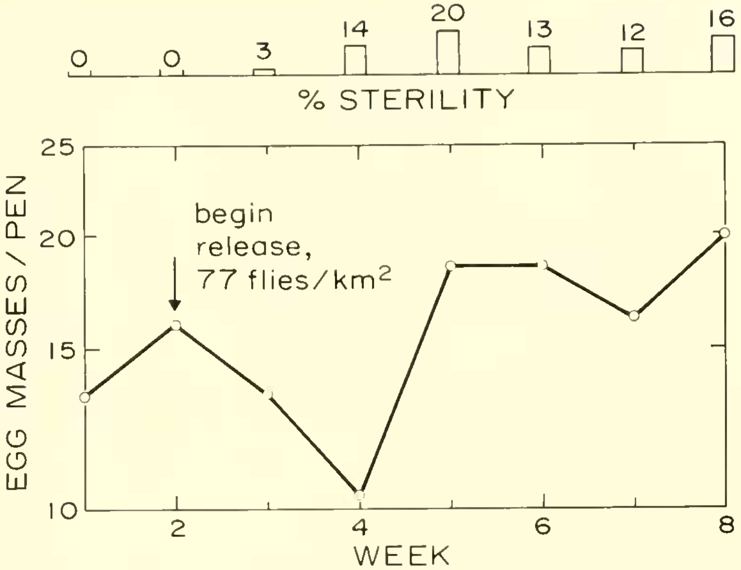

Fig. 2. Curaçao, Netherlands Antilles. Data from first release period at low rate. Two weeks of lower oviposition at 10 sentinal pens followed introduction of sterile flies after week 2. Data from Baumhover et al. (1955).

Baumhover et al. (1959). The 5180 sq km treated area on the eastern coast of Florida between Orlando and Vero Beach contained 8 to 10 goat pens in two groups, each with 2 wounded and 2 healing goats. One of these groups had 4 pens, the other group had 4 to 6 pens. Only the group with a constant 4 pens can be used in this analysis because the number of pens for the other group was changed during the weeks following initial fly release. Three control groups of 4 pens each were located just outside the release area to the north, south, and west. Sterile flies were released via single engine airplane at 386 flies per sq km per week. Initial plans were to treat this area from 2 May to 17 August 1957. Due to rearing problems, however, the area with the constant 4 pens considered here did not receive flies until the week of 12 May. For this reason week 3 is considered the first week of sterile treatment in this analysis.

Trends in oviposition rate for the treatment and control areas are shown in Fig. 3. This experiment had the advantage of a control area for comparison, but as shown in the figure, natural oviposition in that area was considerably below that shown in the test area at the beginning of this test. Another problem with this test was the inexact knowledge of when the first released flies reached the treatment group of pens. Since Baumhover et al. (1959) showed significant sterility in the control pens during the release period, migration of sterile males or sterile-mated native females into the treated area before week 3 may have occurred. If sterile males had entered the area during the first 3 weeks, they had no noticeable effect on oviposition rate. If native females entered this area, the elevated oviposition rate during weeks 2 and 3 may have been due to activity of females "flushed" from the adjacent area.

Clearly, however, reproductive activity of native females was much lower in

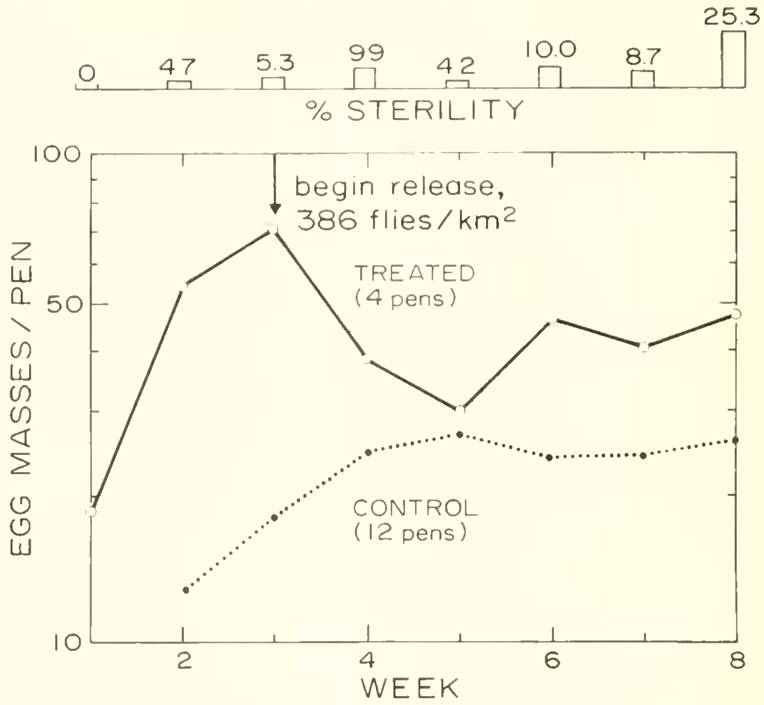

Fig. 3. East central Florida test. Oviposition rate from 4 pens in treated area dropped following release of sterile flies. Control area shows gradual increase in rate for this period. Data from Baumhover et al. (1959).

the release area for the two weeks following direct release of sterile flies. This reduction was not reflected in the activity of the control area females, which suggests that sterile fly treatment was responsible.

Veracruz 1964.—This test was part of a two year series of experiments to examine sterile fly dispersal techniques for eradication of permanent screwworm populations in moist, tropical communities. The region, which was used for field tests in a number of experiments, has been described in detail in publications describing tests following this one (Davis et al., 1968; Krafsur et al., 1979, 1980; Krafsur and Hightower, 1979). The area was centered roughly on Poza Rica, Veracruz and was a 80.5 by 64.4 km rectangle. The area at that time was a mixed agricultural community. Principal land use included banana and citrus groves interspersed with pastures and narrow strips of natural vegetation along waterways and hill tops. Most ranches were small and raised zebu or zebu-brown Swiss cattle. Other animals included horses, pigs and a few sheep and goats at higher elevations. Rainfall during the test period (August to October) was 50 to 75 percent below normal.

Six flight lanes, 12.9 km apart and 80.5 km long were used throughout the tests. Release rate, assuming uniform dispersal of flies, was about 154 flies/sq km/week. Eight sheep pens were used throughout the test and 3 were added during the test. One pen was a control, located 9.6 km outside the test area, and the other added pens were at least 8 km from the nearest pen and probably had little effect on

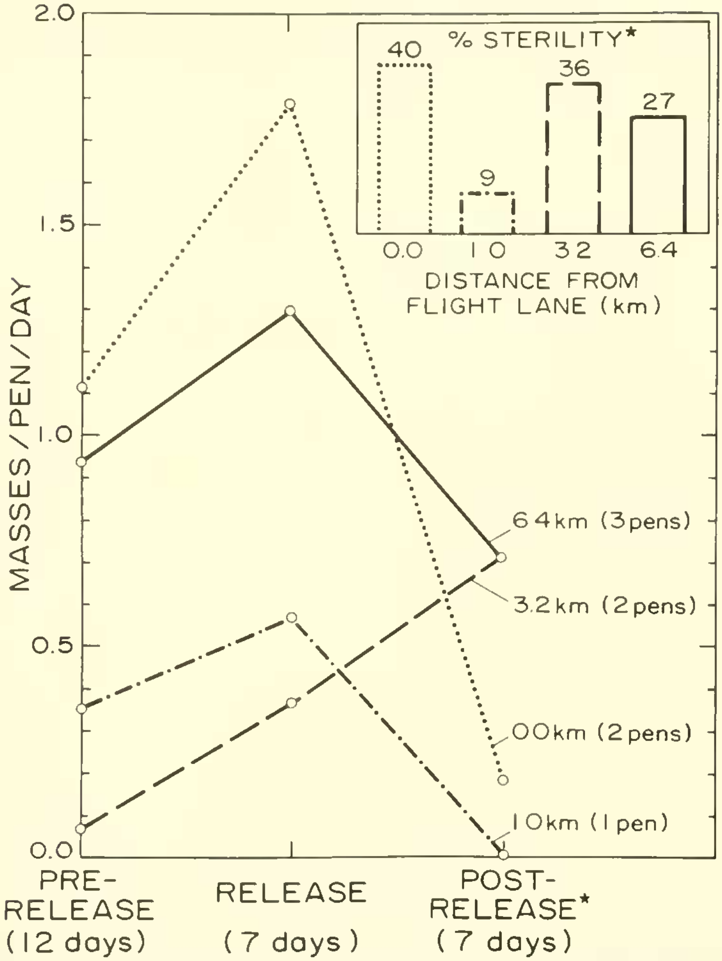

Fig. 4. Veracruz 1964. Oviposition rate increased previous to release, then decreased in 3 of 4 groups following release. The pens not showing an oviposition decrease were those with lowest initial infestation. Data from unpublished USDA report by Davis et al., summarized in Davis et al. (1968).

reproductive activity at the original pens. Only the original 8 pens are used for this analysis.

Results of this test, grouped according to distances from pens to flight lanes, are given in Fig. 4. For approximately 16 pre-release days (July 27 to August 11), there was an increasing trend in rate of oviposition at all pens. For 10 days following the release period there was a decline in egg mass number in 3 of the 4 groups. Only pens located 3.2 km from the flight lanes showed increase in oviposition rate. These pens had the lowest oviposition rate previous to release, suggesting that the sites represented least preferred screwworm habitats. Trapping data given in Davis et al. (1968) indicate that the 3.2 km sites were not attractive to dispersing sterile flies during most of the test, yet sterility at these pens was 36 percent for the total test period; only the 0 km pens with 40 percent had greater sterility. Dry weather undoubtedly had some effect on oviposition rate changes

Table 1. Analysis of egg mass distribution for pens various distances from flight lanes for collections from (I) 19 August to 9 November 1965, and (II) 16 November 1965 to 7 January 1966.

	No. of Pens	No. of Weeks	Total Mean Masses/Wk	Var	Crowdedness	Patchiness
I						
0 km	3	8	32.88	434.90	45.11	1.37
9.6 km	3	8	34.88	188.13	39.27	1.13
II						
0 km	3	13	15.69	126.56	22.75	1.45
4.8 km	3	13	20.23	93.35	23.84	1.18
9.6 km	3	13	26.38	146.08	30.98	1.17

over this time period. Sterility was not a factor in the initial change in oviposition rate as total sterility did not exceed 10% until after 28 August. The coincidence of oviposition decline and release of sterile flies, which resulted in the lowest oviposition rate at pens closest to flight lanes, suggests that sterile fly release inhibited native fly reproductive activity. The increase in numbers of masses at least preferred sites and high sterility at these sites despite a lack of sterile flies, suggests that native females dispersed to the less preferred sites after interacting with sterile flies.

Veracruz 1965 Release Pattern Study.—This study was continued as part of a survey of screwworm ecology for eradication in regions where screwworms are present throughout the year. Pens were set up in the 5180 km sq region centered on Poza Rica, the same site used for the 1964 test, and the tests reported later by Krafsur and Hightower (1979). Flies were distributed from 80.5 km flight lanes separated by 19.3 km with a release rate of about 154 flies per sq km. Pens were located at 0 and 9.6 km from the flight lanes from 21 August until 16 October. Three additional pens were added at locations 4.8 km from flight lanes for the remainder of the test lasting until 14 January 1966. The primary purposes of this test were to compare sterility at various distances from flight lanes and to compare mating success of flies reared on different diets.

Two factors in the design complicate analysis. There was no pre-release sampling and pens were added after the eighth week. However, since pens were set up a known distance from flight lanes and data were recorded separately for pens, the effects of fly introduction can be compared for pens receiving sudden influxes of flies and those more distant from the flight lanes and exposed only to migrant sterile flies. The expectation is that if the native flies respond negatively to sterile flies, fluctuations in reproduction should be greatest for pens located immediately below release lanes. Distribution indices derived by Lloyd (1967), and discussed by Southwood (1978) and Pielou (1977) and others, are used here to compare variability in reproduction rate for pens 0, 4.8, and 9.6 km from flight lanes.

Egg mass distribution is summarized in Table 1 for periods with pens 0 and 9.6 km from flight lanes (I), and with pens 0, 4.8 and 9.6 km from lanes (II). Krafsur et al. (1979) showed that screwworm egg masses are more clumped in distribution in space and time than would be expected by chance. The relationship between mean density (masses/week) and mean crowdedness which adjusts mean density for each mass due to this clumping, is patchiness (Lloyd, 1967). For randomly dispersed (Poisson distribution with variance = mean) egg masses patchiness equals 1.0.

For the first eight weeks after first drop, mean egg mass density is slightly higher for 9.6 km pens. Since there is no pre-release data, the effects of fly release on total mean density cannot be evaluated. Variance in mass number for pens under the flight lanes is 2.3 times greater than that for 9.6 km pens as would be expected if periodic sudden release of sterile flies interfered with oviposition by wild females.

For the last 13 weeks (II), patchiness is also greatest for the pens located under the flight lanes and nearly identical for those 4.8 and 9.6 km from the lanes. During this period 6 drops were made and none were made from October 28 to November 26. Total sterility during the first eight weeks (August 14 to November 9) was 7.9 percent for the 0 km pens and 2.2 percent for the 9.6 km pens. For the second period (II) sterility was 11.2 percent at 0 km pens, 15.2 percent at 4.8 km pens and 5.8 percent at 9.6 km pens. These percentages are not sufficient to explain the variation in numbers of egg masses. Since the patchiness index is independent of mean density (Pielou, 1977), this index reflects the differences in behavior over time rather than changes in native fly density. These trends in oviposition behavior over time are consistent with the hypothesis that sudden increase in fly density interferes with reproduction.

Veracruz 1974.—Following screwworm outbreaks from 1971 to 1973, hypotheses were proposed that screwworm populations were adapting to sterile male treatments in the barrier zone along the U.S.-Mexico border (Smith, 1974; Bushland, 1974). An experiment was performed (Krafsur and Hightower, 1979) to compare egg sterility rates between populations which had been exposed to sterile males for several years in Tamaulipas, Mexico and those in central Veracruz, Mexico which had not recently been treated.

The central Veracruz test is comparable to the other experiments in that the test was performed on a uninured population, treatment rates are known and pre- and post-release data were recorded. The Veracruz experiment, carried out from May to October 1974, involved a treated area of 4000 sq km. Flies of the Tex-Mex strain, then in production for the program, were released weekly by C47 aircraft at a rate of 386 flies per sq km. Egg masses were collected from sheep in 10 pens during most of the test. Oviposition rate was monitored at these pens for 5 weeks previous to release of sterile flies and 11 weeks after release. Egg masses were collected from these sites with some changing of pen location and number, for about a year following this test. As in the 1964 and 1965 tests beef cattle ranches and livestock on small farms were probably the major hosts for screwworms in this region. Details of this experiment as well as the Tamaulipas tests are given in Krafsur and Hightower (1979).

The results of the 1974 test are shown in Fig. 5. Oviposition is given as masses per pen per week. On week 6, the number of pens was reduced from 10 to 9. Ten pens were maintained for the next 11 weeks (Krafsur et al., 1979). The drop in oviposition rate corresponded to sterile fly introduction quite clearly. Weather data did not indicate any sudden changes in rainfall during this period; in fact rainfall averaged 70–75 mm per week from week 6 (18 June) to week 10 (9 July) when the population showed some recovery. As shown in Krafsur et al. (1979), total egg deposition appeared to cycle on a 3 to 4 week period well into the following October.

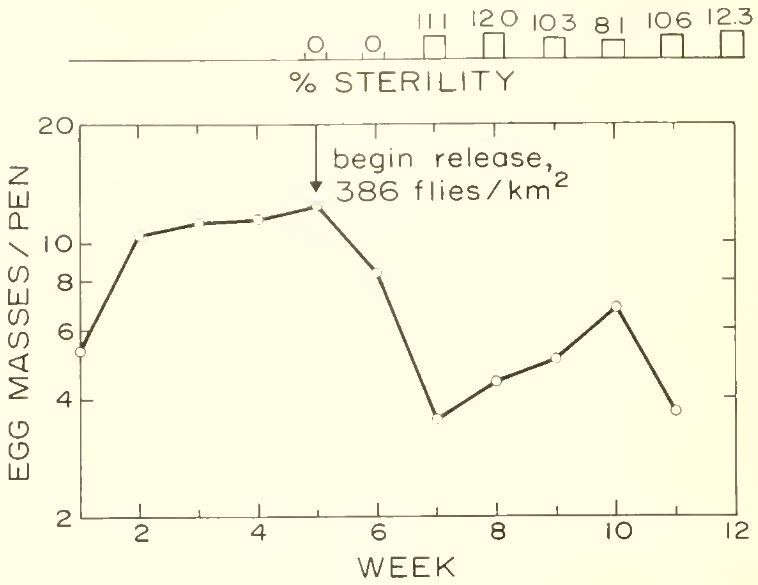

Fig. 5. Veracruz 1974. Oviposition rate per pen for 10 pens decreased following sterile fly release after 4 weeks of relatively stable rate. Data from Krafsur and Hightower (1979).

Sampling in this locality was continued through the fall, winter, and spring 1975. The region was treated again in mid-June. Pre-release means for 1975 were 3.31, 3.85, 5.46 and 7.46 masses per pen per week from 21 May to 17 June. Post-release means were 6.69, 5.85, 5.54, 3.85, 5.46 and 7.46 masses per pen per week from 18 June to 22 July. Comparison of oviposition rate 2 weeks pre-release and 2 weeks post-release indicates only a 3 percent decrease in oviposition. The 1974 and 1975 treatments differed in that, while both used the same mean release density, in 1975 the flies were distributed more evenly, using 3 times as many containers and narrower flight lanes.

Krafsur et al. (1979) present data which suggest a lack of movement of native females among pen locations. There is, therefore, a possibility that since the majority of these pens had been removing egg masses for over a year, the local populations may have been somewhat below the carrying capacity for adult activity including oviposition sites. Population reduction, plus a more even distribution of sterile adults, thus reduced the mean crowding of both sterile and native flies. This was likely to have reduced any negative interaction between sterile flies and ovipositing females.

Sinaloa.—As part of the annual strain-changing routine initiated during the mid-1970's, field evaluations of new strains were performed annually. A new strain derived from Veracruz (DE-9) was tested in Sinaloa, Mexico in 1979. Native flies in this area had not been previously tested with sterile males. The test was carried out in a 5014 sq km area near Sinaloa de Leyva from October to December 1979. Sterile flies were dispersed at a weekly rate of 508 flies per sq km per week with heavier treatments, up to 1000 flies per sq km per week, near rivers or other permanent water sources. Egg masses were collected from wounded sheep in 4 pens during the first weeks of the test. The number of pens was increased to 7

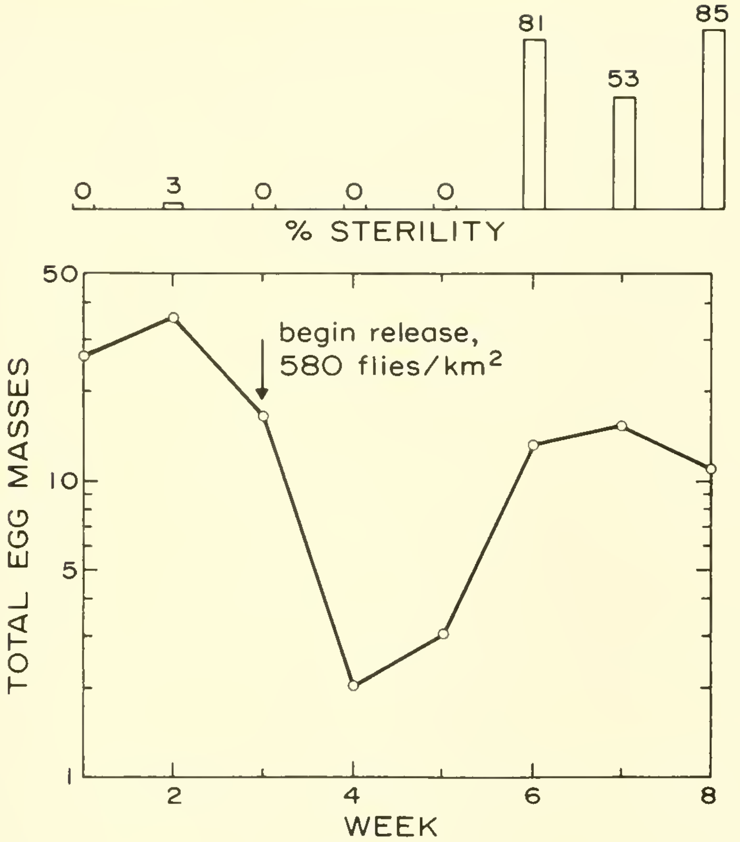

Fig. 6. Sinaloa. Reduction in oviposition per pen following fly release. Pen number ranged from 4 to 7 with pens being added during the fifth week. Data from unpublished report, J. P. Spencer and C. J. Whitten.

during the latter weeks after release. Data were collected for 3 weeks previous to release of sterile flies and 5 weeks after release. In addition to cattle, feral animals, domestic burros and other livestock were likely screwworm hosts in this area. Details of this test have not been published. The test was originally designed to test hypotheses that screwworm populations on the east and west coasts of Mexico were of different genetic makeup and that these differences were reflected in mating behavior. Thus, a strain made up of lines collected in Veracruz was field tested in Sinaloa.

Results of this test are given in Fig. 6. This test involved the heaviest treatment densities of sterile flies discussed this far. The two week decline in egg mass number following this release is also the most drastic. The three week sterility (Fig. 6) achieved and maintained after release is also one of the highest ever achieved. Again, while this evidence consists of only correlative data, the direction of reproductive response to sterile fly release was strong and negative.

Arriaga.—A test to compare mating success in lines of differing genetic derivation was performed in 1981. This experiment compared a broad based strain (V-81) made up by reciprocal, forced crossing of 16 separate egg mass lines from southern Veracruz with a narrow based strain (RGM-6) derived from a single egg mass collected in the Arriaga region of Chiapas.

A test area totaling 4800 sq km was divided into 3 zones along the narrow Pacific coastal plain of Chiapas. Zone A, at the western end near Arriaga, was 76 by 18 km and was treated by RGM-6. Zone B, in the center, was 55 by 18 km and was not treated. Zone C at the eastern end was 72 by 30 km and was treated with V-81. These dimensions were changed during later experiments. Each zone contained 5 sheep pens, wounds were monitored from late April to mid-August 1981. Egg masses were collected for 5 weeks before sterile fly release and 4 weeks after first release at 43 flies per sq km per week. Some pens were moved the first week in July and a higher release rate of 125 flies per sq km per week was used for 4 weeks. Potential host animals in this region were mainly cattle belonging to large ranching operations. Domestic dogs, swine and other animals were numerous near villages and ranch buildings. Feral dogs provided additional substrates particularly near six towns (pop. 15,000–40,000) located within the test region.

Results of this test are discussed in McInnis et al. (1983), mainly from a cytogenetic standpoint, and are reviewed in Richardson et al. (1982a). Rates of oviposition are summarized in Fig. 7. During this test extreme fluctuation in weather, particularly due to storms from the Pacific Ocean, resulted in large fluctuations in both daily and weekly oviposition rates. Reproduction is therefore summarized as egg mass number in the treated area minus that in the control. As indicated in Fig. 7, zones A and C had weekly fluctuations which were independent from each other until the week of release. For two weeks after release both zones were far below the control in screwworm activity; for the next six weeks the two zones were again independent from each other. In this test there is some indication that females may actually leave areas that are inundated with sterile flies. The rate of sterility in the untreated zone was higher for the period immediately following release than either of the treated zones. Since total number of egg masses also increased during this period in zone B (McInnis et al., 1983), native females mating to sterile males and migrating into this zone from the adjacent treated areas were the likely causes of this sterility and increase in oviposition.

Guerrero.—Iso-female lines collected during the Arriaga test were combined by "fly choice" (lines of the same adult age combined without separating the sexes) to produce the A-82 strain. This strain was field tested in Guerrero, Mexico, east of the town of San Marcos, centered on the 99th degree longitude line. The test area was roughly rectangular (30 by 50 km) with the long side parallel to the Pacific coast. The southern boundary of the area was about 3 to 10 km from the coast.

A variety of potential hosts inhabiting this region included goats, swine and cattle belonging to small agricultural operations. Feral and domestic dogs, cats and burros were also potential hosts. Ten corrals were set up containing infested animals. These included a total of 30 sheep, 3 goats, 3 cows, 3 pigs, and 1 horse. These pens were located in the southern part of the test area with at least 2 pens outside the zone of sterile fly release. Wounded animals were monitored for 2 weeks before initial sterile fly release. Flies were released from a single engine plane from 11 July to 19 September, 1982. For the two weeks in July, release rate

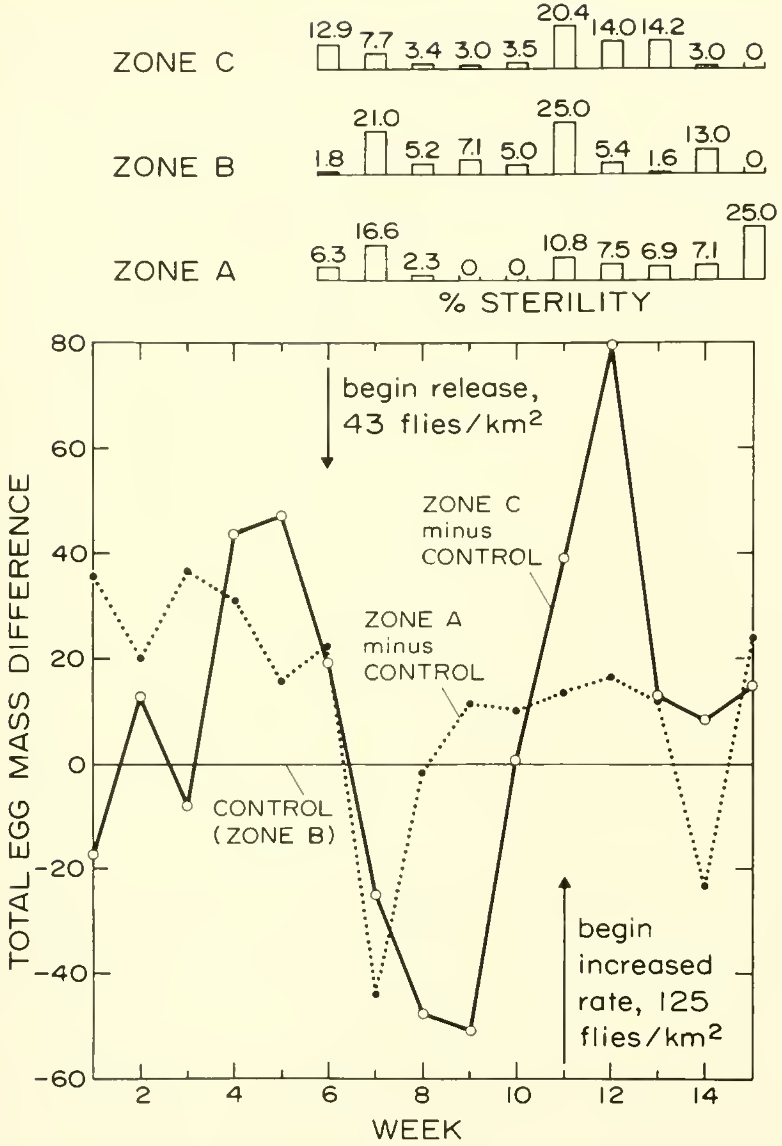

Fig. 7. Arriaga. Difference between oviposition rates in treated (A, C) and control (B) zones before release and following release at low and high rates. Each zone had five pens. Rates in both A and C decreased relative to B following release, flies from treated zones may have been flushed into control zone. Data from McInnis et al. (1983).

was 298 and 338 flies per sq km, for all remaining weeks release rate was greater than 412 flies per sq km.

Fig. 8 gives the rates of oviposition and sterility for this test. The two large drops in oviposition rate are both associated with introduction of sterile flies. Rate of oviposition before introduction of sterile insects was extremely high, probably reflecting the lack of care given the relatively high density of domestic animals in the region. The sudden apparent decrease in oviposition during the week of July 8 to 14 was not associated with any obvious weather changes. Captures in wind oriented traps using an adult attractant (Swormlure-4) also decreased drastically during this period. The drop from week 5 to week 6 coincides with the introduction of sterile flies at approximately 50 percent higher density. These data appear to be in mild agreement with the hypothesis of density dependent interference in reproduction. This test was carried out during a period of extremely high reproductive activity and population fluctuation, partly due to the onset of the rainy season (see Spencer et al., 1981; Krafsur et al., 1979). Baumhover (1963) showed, with laboratory tests, that pupae are highly susceptible to low humidity (<40%), oviposition increases following onset of rainy season are likely to have been due to increased survival of pupae in moist soil. These fluctuations, especially the drop at week 3, could be responses, at least in part, to other factors.

The next group of field tests include 3 tests executed in areas which were part of the eradication barrier or were performed in regions as a continuation of a previous experiment. These areas were generally at the southern margin of the eradication zone or in regions previously described here. Again, sites were chosen with respect to accessibility and high screwworm activity. These tests are of particular interest in that they provide insight into the probability that native populations change their distribution or behavior after sterile fly introduction in a manner which allows them to reproduce at their pre-release rate. Unfortunately, tests in which treatments were monitored in a comparable manner to the tests on uninured populations all have weaknesses which preclude simple comparisons. I include these tests here as illustrations of the possible types of responses that may be shown by treated populations with the admonition that these data have major deficiencies.

Tamaulipas A and B 1974.—These adjacent areas were located at the southern edge of the barrier zone being maintained along the United States-Mexico border. Details of the design and purpose of these tests are given with the Veracruz 1974, summary in Krafsur and Hightower (1979). Two sites, measuring 64 by 80 km were oriented such that flight lanes were directed north and south and separated by approximately 4 km. Zone A, centered on San Fernando, and zone B, centered on Soto la Marina, were treated with sterile flies of the currently used Tex-Mex (zone A) and newly constituted FF8 (zone B) strains respectively, at 386 total flies per sq km per week. Drop rates were planned to be from mid-June to late August, with 11 weekly releases. Actual releases were reduced by weather conditions such that the first 4 releases in zone A and the first 5 releases in zone B were poorly targeted or missed the zones.

Results of these tests and other tests in areas previously exposed to sterile flies are summarized in Table 3. Total masses per pen per week are averaged for pre- and post-release weeks. For post-release data, the 2 weeks following release are averaged since this represents the period when reproductive activity has been shown to drop in untreated populations.

Comparison of the pre-release and post-release means for these two areas indicates that no decline in oviposition rate resulted from sterile fly introduction. Whether this indicated that the population was below adult carrying capacity, that native flies were acclimated to inundation by sterile flies, or that the problems

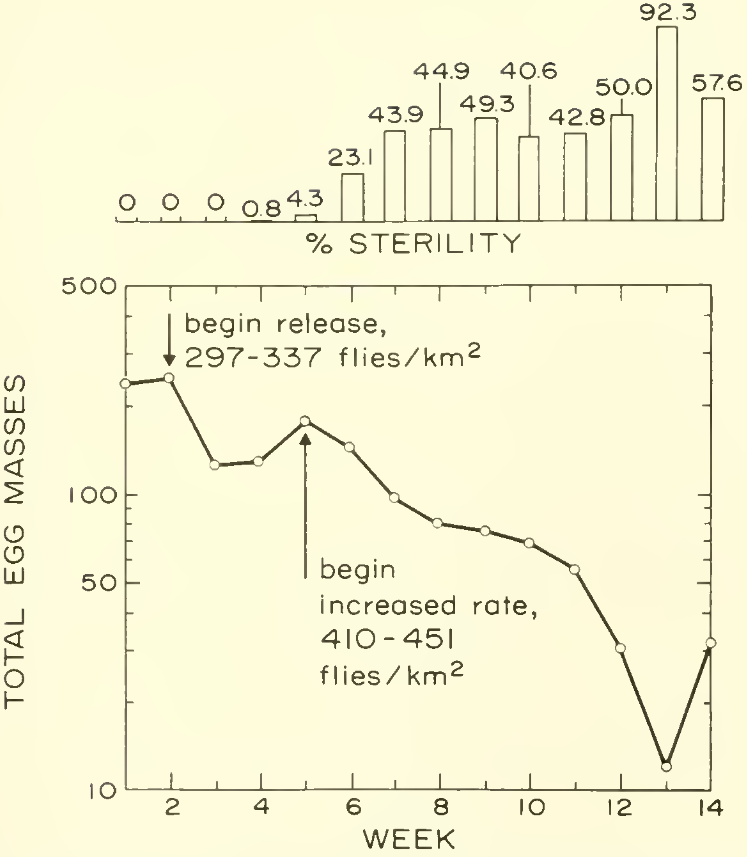

Fig. 8. Guerrero. Total masses collected per week from ten corrals containing various animals. Two release rates were used, a two week decline occurred following the low release rate then began a steady decline following the second, higher rate. Data from unpublished strain evaluation report, Comision Mexico-Americana (1982).

in release had resulted in a gradual increase in fly density to which the native flies adapted, cannot be determined.

Veracruz 1980.—This test involved release of a strain of sterile flies derived from the west coast (Sinaloa) of Mexico in an area on the east coast. This was a reciprocal of the Sinaloa (1979) test for genetic differentiation of geographically isolated populations. The test area, south of the city of Veracruz, had been the site of several field tests of sterile flies and attractants. Sterile flies had been released at this site as part of the eradication program, capture rates of 0.14 sterile flies and 0.09 fertile flies per trap per week were recorded before introduction of the Sinaloa strain. Flies were released at about 579 flies per sq km per week over a 2331 sq km area. The test was performed from July 4 until 14 August 1980. Initial release date was 15 July 1980. This test, while achieving its purpose of field testing a candidate strain for plant production and testing for geographically based mating barriers, did not provide conclusive results relative to the effects of sterile flies on oviposition rates. A major problem involved changes in experi-

Table 2. Summary of field tests in regions previously treated with screwworms or manipulated to reduce screwworm density.

Test Locality	Year	Pre-release Masses/Week	Post-release Masses/Week	Total Sterility %
San Fernando, Tamps.	1974	55	72	36.6
Soto la Marina, Tamps.	1974	55.3	60.5	30.5
Veracruz	1980	19	35.5	49.5
Arriaga V81	1981	59.5	91.0	11.5

mental design during the test. The pen receiving the second largest numbers of egg masses was initiated the day before first drop. This pen was located at the same ranch as the pen receiving the most egg masses; the likely interaction between pens perhaps biases any estimate of the effect of fly release even when this new pen is omitted from the data. In addition to the changes in pen number, this test was initiated during the beginning of the rainy season when screwworm populations are known to increase in the tropics (Spencer et al., 1983), and the test could not be performed to the planned conclusion due to hurricane Allen.

Despite these conditions, data in Table 2 show that considerable sterility was achieved; thus the sterile flies were successfully interacting with native flies. Without a control area, during this period of naturally changing population structure, the conclusions concerning the effects of sterile fly inundation are tenuous. It may be concluded, however, that this test did not show a decline in oviposition rate due to sterile fly release.

Arriaga V81.—Following the Arriaga test of genetic lines discussed above, a field test was performed in the same region, using nearly identical pen sites from 10 August to 7 November 1981. This test, designed to evaluate the performance of the V81 line as a strain for plant production, was carried out at release densities approximating those used in the eradication program.

The test was carried out in two stages, the first using zone B as an untreated control zone as in the comparison test; the second stage was executed without a control zone and with pens moved to new locations. Since the second stage of this test followed the first stage with only two nonsampling days, there were no pre-release data and no control pens. Data from the second stage are not included in this study.

Results of this test, shown in Table 2, indicate that there was no reduction in oviposition rate either in absolute numbers of masses or in the difference between treated and control areas. While the sterility in this region seldom exceeded 10 percent during the strain comparison test, that level of sterility and the removal of egg masses from 25 April until the initiation of this test may have reduced population density to a level below that which would result in reduction of native fly reproduction. It is at least equally probable that after more than 3 months of sterile fly treatment, the native population had acclimated to sterile flies in the region.

DISCUSSION

Natural populations of screwworms were shown in these tests to have reduced reproductive activity in response to sterile fly inundation. The response is tem-

Table 3. Summary of effects of sterile fly release for field tests with oviposition data collected before and after release.

Test Site	# Masses Before Release	# Masses After Release	% Drop	Sample Period*
Sanibel	22	10	55	1 week
Curaçao	288	238	17	2 weeks
Florida	497	270	46	2 weeks
Veracruz 1964	106	55	48	10 days
Veracruz 1974	240	110	54	2 weeks
Veracruz 1975	168	163	3	2 weeks
Sinaloa 1979	46	13	72	2 weeks
Guererro 1982**	536	254	53	2 weeks
Guererro 1982***	286	165	42	2 weeks

* Period of time pre- and post-release.
** For weeks before and after actual release.
*** For weeks before and after first released flies were trapped.

porary, lasting about two weeks. Evidence from nine tests on populations in regions of heavy screwworm infestation indicates that this reduction in oviposition rate is consistent and normally occurs before there is significant sterility. This suggests that the interaction between mated native females and introduced sterile flies caused this reduction.

In two tests carried out in a barrier zone (Tamaulipas A and B) where sterile flies had been released on a regular basis, and two tests where populations had been disrupted by previous sterile fly introductions (Arriaga V81) or long term heavy sampling (Veracruz 1975), there was no reduction in oviposition rate as a response to sterile fly introduction. These results suggest that some sort of density dependant interactions or changes in behavior patterns occur when population density is increased.

Possible types of interactions responsible for this response are competitive interference at oviposition sites or adult feeding sites. Since flies reared from eggs collected in the field can feed at densities of 200–300 flies on a few square centimeters of food or moist cotton, and crowding the females in small (6 dram) vials stimulates oviposition, interference competition does not appear to be responsible for the drop in reproductive activity. This increase in adult density is not likely to cause resource depletion since both liver trap and swormlure trap data indicate that screwworms make up less than 1% of adult Calliphoridae in natural communities.

Observations of sterile flies (Guillot et al., 1978; Krafsur, 1978; Mackley and Long, 1983) indicate that both sexes are attracted to flowering trees and shrubs. Observations of fertile flies indicate that only females are attracted to wounds, though not all females collected on wounds contain mature eggs (Guillot et al., 1977a). Native females spend minimal time around wounds. Oviposition is initiated within a minute after a female lands on a wound, the female feeds on fluids before and during oviposition and leaves immediately after oviposition. I have observed up to 3 females simultaneously ovipositing on a single wound with an opening of less than 2 cm sq. Guillot et al. (1977a) report that females may orient toward other ovipositing females, then commence oviposition. Since females typically mate once, most activities by mated females are probably associated with host and nutrient location. Male efforts are apparently mainly expended on mating at sites where both sexes feed. I have found no evidence, either in the literature or in field observations, indicating that inter-female competition occurs at wound sites.

A logical and, I believe, likely cause of the reduced oviposition following release is a change in behavioral structure of the native population induced by changes in total population density. While screwworm females are capable of moving great distances under certain conditions (Barrett, 1937), data collected from high infestation regions in Veracruz (Krafsur et al., 1979) and Chiapas (Brenner, 1984) suggest that little dispersion occurs during periods of optimal local environmental conditions. Evidence from Florida 1957, Veracruz 1964 and Arriaga suggests that the influx of sterile flies is correlated with dispersion of native females resulting in a net emigration of native females away from the release zone.

Mating behavior in screwworms is apparently initiated by males striking from perches on flowering shrubs and trees. Females are grasped (this is called striking in screwworm jargon) in midair, the pair falls to the ground where the female is either released or copulation lasting about 2 minutes occurs (Krafsur, 1978; Guillot et al., 1977a). Other flies are frequently struck by males but are immediately released. In laboratory cages, mortality rate for females caged with males greatly exceeds that of females caged alone. In a study by Guillot et al. (1977b), reproductively young females differed significantly from older females in their response to baits and host animals. Virgin females were significantly less attracted to host animals than to liver or chemical attractant baits.

In the natural populations studied here, egg masses were collected at a rate ranging from about 10 to 50 masses per pen per week. Assuming that half of these masses are from the first gonadotrophic cycle, 5 to 25 females per week visit pens for deposition of their first egg mass. If male courting sites attract females at a similar rate, this number represents a maximum estimate of the number of encounters per week for a courting male. That is, a male would have 1 to 4 opportunities per day to compete for females approaching a courting site. Parker (1974) has shown that courting effort (persistence) is optimized if it is proportional to time between courting opportunities. If male screwworms are optimizing their courtship efforts, they would be expected to expend maximal effort for each encounter since encounters are relatively rare.

Baumhover (1965), Crystal and Ramirez (1975), Crystal and Whitten (1976) and others have shown that as screwworm strains undergo adaptation to laboratory or production rearing conditions, their courtship becomes more aggressive, that is, females caged with males from older laboratory lines die at a faster rate than females caged with newly colonized strains. The result of high density sterile fly release is then to create a community in which females are being struck by males at a higher rate and perhaps more aggressively than normal. Since the majority of these males are released on grid patterns, any localization of native males existing before sterile fly release is swamped out. Native females have no way of avoiding this courtship except to migrate or seek refuge.

Evidence from most of these field tests and experiments indicates that for moderate to high release rates, i.e., exceeding 300 flies per km sq, a drop in oviposition rate of 50 percent may be expected. This effect appears to last for about 2 weeks, then recovery may occur (Curaçao, Florida 1957, Veracruz 1974, Sinaloa 1979) but not always (Guerrero, 1982). Program managers might take advantage of this effect by first flooding new areas with a much higher initial rate of flies than normal., 500 to 1000 flies per sq km for example, to achieve maximal interference. Then by calculating when unmated females from the recovery generation are expected to appear (approximately 3 to 4 weeks later), a second massive drop could be made to insure that these females are courted by sterile males so further interference may occur.

Another possible advantage of this interaction is in stopping migration of fertile flies into or across a barrier zone such as is in place at the Isthmus of Tehuantepec in Mexico. While theoretical studies of sterile release dynamics have claimed to demonstrate maximum release rates, above which additional releases are not effective (Costello and Taylor, 1973), several tests have shown that sterility in a test zone can be maintained at a higher rate when density of released flies is excessive, such as during the Sinaloa 1979 test. Brenner (1984) showed that a significant difference in sterility rate could be maintained between pens inside and outside a release zone, separated by less than 40 km, if ground released sterile fly density exceeded 2000 flies/sq km/week but no difference was observed when release rate was less than 1000 flies/sq km/week. Maintenance of a barrier zone might be greatly enhanced if massive releases within the barrier are adjacent to outbreak zones outside the barrier.

In this discussion I have inferred, mainly from laboratory evidence and indirect interpretation of field data, that the interactions between wild and released flies are either directly behavioral or of the interference type. Monro (1966) suggested in experiments with the fruit fly *Dacus tryoni* Frogg that native flies were flushed by introduced flies due to competition for space or some other consumable resource. This is not likely for screwworms since no evidence suggests they ever reach stable equilibrium or saturation densities relative to adult resources. The temporary (2 week) nature of this interference in most tests further indicates that the mechanism of eradication is due to sterility and not interference alone. During the period of screwworm eradication, extensive attention has been given to genetic interpretations of population interactions (Smith and Borstel, 1973; Smith, 1974; Bushland, 1974; Bush et al., 1976; Richardson et al., 1982; McInnis et al., 1983). Few published works, other than reports of field tests of new strains, have dealt with population dynamics of released plus native screwworm adults (Krafsur et al., 1980; Krafsur and Garcia, 1978; Brenner, 1984). The temporary interruption of reproductive activity demonstrated in the tests discussed here may, however, prove useful if integrated into the dispersal schedule and pattern for reaching and maintaining a screwworm barrier.

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